



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE GEOTROPISM OF THE SEA-URCHIN *CENTRECHINUS*.

G. H. PARKER,

ZOOLOGICAL LABORATORY, HARVARD UNIVERSITY.

The long-spined sea-urchin, *Centrechinus antillarum* (Phil.), is abundant on the flats near the Miami Aquarium in Biscayne Bay, Florida. It is a common object of interest in the aquarium tanks, where it is found climbing up the stone-covered walls or perched on the top of the submerged rock-work. When transferred to a large glass jar filled with quiet or running sea water, it immediately starts to climb up the sides of the vessel, and each time it is loosened and dropped to the bottom it renews this activity. This response occurs in the dark as well as in the light, and in vessels the water of which is cut off from the air by a glass plate as well as in those whose contents are exposed to the air. In other words, *Centrechinus* climbs upward, not because of light or of access to oxygen, but in response to gravity. It is a strongly geonegative animal.

Centrechinus belongs to the group of regular sea-urchins, but, like most representatives of this group, its radial symmetry is disturbed by the single madreporite which occupies the aboral end of one of its five interradial zones. Thus a structural axis of orientation is established. As *Centrechinus* is remarkably active in its geotropic responses, it is a favorable form with which to test orientation in locomotion. Does it move as bilateral animals almost always do, with one end of a definite axis constantly forward, as, for instance, the one marked by the madreporite, or may any of its numerous axes serve as a line of progression? This general question has already excited the attention of a number of students of the echinoderms.

Jennings (1907, p. 155) states that the California starfish, *Asterias forreri*, "may move with any one of its rays in the lead, or with any interradius in advance, or indeed in any intermediate direction, so that its possibilities as to variations of direction of

locomotion are really unlimited." Cole (1913) in his study of the New England starfish, *Asterias forbesi*, demonstrated in this species the same unlimited possibility of direction of locomotion that Jennings had done for *A. forreri*, but Cole further showed by means of statistical methods that *A. forbesi* moved more frequently with that part forward which was in close proximity to the madreporite than with any other part. He, therefore, established what has been called a physiological anterior for this species, an anterior that corresponds almost exactly with that assumed on different grounds by Lovén for echinoderms in general. Cole's observations form, as a matter of fact, a rather remarkable confirmation of Lovén's deductions.

Agersborg (1918, p. 233) in his study of the habits of the twenty-rayed starfish of the Pacific coast, *Pycnopodia helianthoides*, calls attention to its bilateral tendencies and states that it does not readily move backward or sidewise, but uses the side established as fore end always as anterior end. He, however, nowhere makes really clear how its physiological bilaterality is related to its structural bilaterality. If they agree, as his account seems to imply, then the physiological anterior of *Pycnopodia* must be different from that of *Asterias*, judging from the account of the structure of *Pycnopodia* given by Ritter and Crocker (1900). In *Asterias*, according to Cole, the physiological anterior centers on the arm to the left of the madreporite as viewed aborally (III. in Lovén's system). In *Pycnopodia* it appears to center on the second arm to the right from the madreporite as viewed aborally. Thus the axis of locomotion in *Asterias* is two fifths of a circumference from that in *Pycnopodia*. But this conclusion is based on statements of structure from Ritter and Crocker and of habits from Agersborg, both of which may be open to fundamental revision. So far as *Pycnopodia* is concerned, the one thing that in reality seems certain is that it has a physiological anterior, but how this is related to its structure remains to be ascertained.¹

The Bermudian starfish, *Coscinasterias tenuispina*, has been studied in its methods of reproduction and of locomotion by Crozier (1920a). This species propagates by division and conse-

¹ This subject is not greatly clarified in a second paper recently published by Agersborg (BIOL. BULL., vol. 42, p. 202).

quently a given individual may have more than one madreporite as a preparatory step to division and may have arms of different length as the result of regeneration after division. Crozier studied the locomotion of *Coscinasterias* in relation to the length of the arms and the position of the madreporites and found that both factors had an influence in determining the axis of motion. Although the animal could move in any direction, there was an obvious tendency to move more generally in the direction of the long arms and on the axis determined by the position of the madreporite, and of these two factors the position of the madreporite on the whole predominated. Thus in all the starfishes that have been investigated in this respect a physiological anterior has been discovered, and this anterior seems to find a structural indication in the position of the madreporite whereby an arm next this organ commonly becomes a director.

Among the crinoids Clark (1915) has shown that *Comatula purpurea* moves with its long arms anterior, but whether the axis thus established agrees with that in the starfishes can not be ascertained because of the absence of the madreporite from crinoids. *Comatula* must, however, be admitted to possess a physiological anterior.

Few observations have been made on the direction of locomotion in the sea-urchins. Holmes (1912), in his study of the phototropism of *Arbacia*, describes the locomotion of this sea-urchin as though it were free to move in any direction, yet he makes no specific statement on this point. Crozier (1920b), who studied the bionomics of the sand-dollar, *Mellita*, found that this animal had a very definite axis of locomotion which corresponded with its structural axis of bilaterality. In *Mellita*, as in other sand-dollars, the mouth is at the center of the underside of the disc, but the anus is on the edge of the disc in an interradial position. A line drawn through the anus and the center of the disc in *Mellita* marks the axis of locomotion and the forward end of this axis in creeping and in digging is the end farthest from the anus. The madreporite in the sand-dollar is central in position and hence can not be used in homologizing rays as in other sea-urchins, but by comparing the conditions in *Mellita* with those in the spatangoids, in which the symmetry is also bilateral but the madreporite is excentric, it can

be shown that the ray in the sand-dollar that is opposite the anus is the homologue of the ray in *Asterias* that is to the left of the madreporite and that serves as the director in locomotion. Hence the axis of symmetry and direction of locomotion in *Mellita*, as determined by Crozier, are in agreement with the conditions in *Asterias* as determined by Cole. This is a rather striking correspondence in both anatomical and physiological details.

Although the radial symmetry of the echinoderms expresses itself in the ability of these animals to move in any direction in the horizontal plane, yet in the few instances studied there seems to be also a marked tendency toward a physiological anterior which takes its origin from the position of the madreporite and is in agreement with the structural bilaterality of the spatangoids and the clypeastroids.

To test these relations in the regular sea-urchin *Centrechinus* a bit of white thread was tied to a spine on the ray to the left of the madreporite (III. in the Lovén system) and, with this ray thus identified, the sea-urchin was allowed to climb the sides of a glass jar ten times and the position of the axis of locomotion in relation to the given ray was recorded for each ascent. Tests of this kind were made on four animals. These animals, after an ascent had begun, showed little of the circling movement observed by Crozier (1920b) in *Mellita*, but maintained a fairly constant relation between the axis of locomotion and their structural axis over a vertical course of some 40 centimeters. It was not always easy to observe the exact relation of the structural axis of the animal, as indicated by the marked spine, to the direction of locomotion, but this relation is accurately enough indicated in terms of rays, though the animals may have crept at times more nearly interradially than radially. Records were kept by noting which ray was nearest the physiological anterior during the test. The results are shown in Table I.

Two conclusions may be drawn from Table I. First, there is nothing about the records in this table that suggests that *Centrechinus* has a physiological anterior. The ray III., that might be suspected in this respect, is in no sense a director, in fact it is rather the reverse. It is, however, perhaps open to doubt whether there is a sufficient number of observations in the table to warrant

any sound conclusion whatever on the question of a physiological anterior. But so far as these records go, there seems to be no suggestion of this state in *Centrechinus*.

TABLE I.

NUMBER OF TIMES IN TEN TRIALS ON EACH OF FOUR SEA-URCHINS (*Centrechinus*) THAT A GIVEN RAY WAS FOREMOST IN GEONEGATIVE LOCOMOTION.

The rays are numbered according to the Lovén system, the ray opposite the madreporite being V, the one to the right of this ray being I, and the others following in sequence around to V.

No. of Animal.	No. of Ray (Lovén's System).				
	I.	II.	III.	IV.	V.
I.....	2	2	1	3	2
2.....	2	3	2	2	1
3.....	2	1	3	3	1
4.....	3	2	1	1	3
Totals.....	9	8	7	9	7

The second conclusion to be drawn from Table I. is abundantly supported by the observations. This conclusion is to the effect that *Centrechinus* is able to carry out geonegative responses on any axis in its body. This conclusion is unquestionable and shows that the geotropism of *Centrechinus*, unlike that of a bilateral animal, is performed without initial orientation and, as a type of sea-urchin locomotion, it is not necessarily associated with any particular ray. In this respect the geotropism of *Centrechinus* is much more like that of a plant than like that of most animals in which the axis of the animal is first moved so that the creature heads either toward the center of the earth or away from it, after which locomotion in the appropriate direction takes place. In *Centrechinus*, as already intimated, no initial orientation occurs, but the sea-urchin with any axis forward creeps upward. This condition emphasizes what Loeb long ago pointed out, the essential similarity between the tropisms of plants and of animals.

When an attempt is made to analyze the geonegative responses of *Centrechinus*, it is found to be no simple problem. These responses involve stereotropism as well as geotropism and the latter in its more generalized type such as occurs in plants. If a *Cen-*

trechinus is dropped so as to rest with its side or its aboral face on the horizontal floor of an aquarium, an activity of spines and ambulacral feet ensues which eventually rights the animal in that its oral side is brought next the aquarium floor. Not till righting has been accomplished does locomotion in the proper sense begin. I never have seen a *Centrechinus* progress on its back or its side, but only with its oral surface next the substrate. It has often been assumed that in echinoderms the righting reaction is a response to gravity, but this is doubtful, in *Centrechinus* at least, as the following experiment shows. If a strong thread is tied round the equator of a *Centrechinus* and the animal is suspended in an aquarium so that its side touches the vertical glass wall, the spines and feet will begin the same kind of movements that they did when the animal rested on its side at the bottom, and in a short time the sea-urchin will have its oral surface applied to the vertical face of the aquarium as it formerly did to the floor. Since in this test the axis of the sea-urchin is at right angles to the direction of gravity instead of being parallel to it as in the ordinary righting reaction, it is clear that righting is not a response to gravity, but to a solid surface against which the creature comes always to apply its oral side. Righting in *Centrechinus*, therefore, though apparently geotropic, is in reality not so, but stereotropic. On this point my results confirm those of Moore (1910), who has described a similar condition in the starfish. In discussing the geotropism of *Centrechinus*, therefore, the righting movements are not to be considered, for they belong to a different category of reactions; they are reactions to solid surfaces. In this respect *Centrechinus* agrees with *Planaria*, whose righting reactions are apparently also stereotropic (Pearl, 1902), though this worm likewise shows true geotropism (Olmsted, 1917).

After a *Centrechinus* has obtained a footing on a vertical surface, it does not wander indiscriminately over this surface, but it travels up the surface against gravity. It is this reaction that is indicative of true geotropism and that still requires to be considered.

Two general theories have been advanced to show how geotropic responses are accomplished: the so-called mechanical theory apparently first proposed by Aderhold (1888) and advocated by Ver-

worn (1889) and the statocyst theory put forth by Lyon (1905) and espoused by a number of later workers, Kanda (1914) and others. According to the mechanical theory the weight of the body of the responding organism is so disposed in relation to the locomotor apparatus that the creature is kept mechanically headed either toward the center of the earth or away from it. In this way the action of gravity on the body as a whole determines the direction of locomotion. In such cases the organism would maintain the same orientation dead or alive. Few, if any, instances of this kind have ever been found, and though it must be admitted that every organism is always under the direct influence of gravity and varies in weight in different parts of its body, practically none have been found that exhibit conditions favorable to this view. *Centrechinus* with its symmetrical distribution of parts gives no suggestion of a preponderance of weight on one side or the other, and the fact that it may assume a new axis with almost every ascent on the aquarium wall is a condition extremely difficult for the mechanical theory to meet.

The statocyst theory assumes that within the body of the organism there are movable masses of higher specific gravity than their fluid surroundings, and that these masses under the influence of gravity press upon one side or the other of their containing chambers in accordance with the position of the organism in relation to the center of the earth. To these pressures the organism then responds in an appropriate way. Organs acting in this fashion and known as statocysts with their contained statoliths occur commonly among such animals as the worms, the mollusks, and the crustaceans.

This theory is also believed to apply to the simpler animals and to the plants in that geotropism is excited in these organisms by the pressure exerted by small particles contained within the vacuoles of their protoplasm. This view is supported by such observations as those of Zollikofer (1918) on the seedlings of certain compositæ. When these seedlings are placed in the dark for three or four days, the starch grains in their hypocotyls disappear, and with the disappearance of the starch the geotropic reactions of the seedlings cease, though the seedlings seem not to have suffered from the treatment, for they are still phototropic. Apparently the

starch grains act as statoliths in the spaces in which they are lodged. In this way the small solid particles in the protoplasm of the simpler animals and plants are supposed to render these organisms geotropic.

As a refinement and extension of this view, Small (1920) has suggested that under gravity the disperse phase in the protoplasm of geotropic organisms moves to one side of their bodies, a process analogous to creaming, and thereby brings about a change in electrical potential which results in geotropic movements. As an objection to this view Blackman (1921) points out, among other things, that creaming is a slow process, and that geotropic response is often quick. Certainly in *Centrechinus* such a response can occur in less than a second, as can be shown by tilting into the vertical a horizontal plate of glass on which a sea-urchin is creeping. Hence creaming can scarcely explain the geotropism of the sea-urchin.

How this is to be explained is not a simple matter, for *Centrechinus*, so far as is known, is entirely devoid of statocysts, and even assuming that it possessed them, the fact that it progresses upward with any axis forward is a difficult feature to explain. Nevertheless its body is provided with a number of parts whose action may make clear how its geotropism is accomplished. Such parts are the spines and the ambulacral feet. They are heavier than the sea water in which they are immersed and in consequence of their weight tend to hang down from their supports. This is especially true of the spines, which are heavily impregnated with lime and provided with ball-and-socket bases. In fact, these organs are beautifully arranged to respond to the pull of gravity and, assuming that their bases are provided with a nervous mechanism sufficiently differentiated for the purpose, they might perfectly well serve as organs for the initiation of the response to gravity. In that case the stimulus would be the deforming pressure exerted at the base of the spine by its movement under the pull of gravity. It is a deforming pressure of this kind that acts as a stimulus and not a general pressure such as fluids exert and as was believed to be effective in geotropism by Jensen (1893). A deforming pressure, if exerted locally at the base of the spine, might well excite in a differentiated system of basal receptors impulses to locomotion

that would result in an appropriate geotropism. Such a form of response is in essence that implied in the statocyst theory in which the stimulus must be a deforming, not a general, pressure. But whether in *Centrechinus* it is the spines or some other similarly constructed organ that initiates the geotropic response remains to be ascertained.

REFERENCES.

Aderhold, R.

- '88 Beitrag zur Kenntnis richtender Kräfte bei der Bewegung niederer Organismen. *Jena. Zeitschr. Naturwiss.*, Bd. 22, pp. 310-342.

Agersborg, H. P. K.

- '18 Bilateral Tendencies and Habits in the Twenty-rayed Starfish *Pycnopodia helianthoides* (Stimpson). *BIOL. BULL.*, Vol. 35, pp. 232-254.

Blackman, V. H.

- '21 The Theory of Geotropic Response. *New Phytologist*, Vol. 20, pp. 38-42.

Clark, H. L.

- '15 The Comatulids of Torres Strait: With Special Reference to their Habits and Reactions. *Carnegie Inst., Washington, Publ.* 212, pp. 97-125.

Cole, L. J.

- '13 Direction of Locomotion of the Starfish (*Asterias forbesi*). *Jour. Exp. Zool.*, Vol. 14, pp. 1-32.

Crozier, W. J.

- '20a On the Temporal Relations of Asexual Propagation and Gametic Reproduction in *Coscinasterias tenuispina*: with a Note on the Direction of Progression and on the Significance of the Madrepores. *BIOL. BULL.*, Vol. 39, pp. 116-129.

Crozier, W. J.

- '20b Notes on the Bionomics of *Mellita*. *Amer. Nat.*, Vol. 54, pp. 435-442.

Holmes, S. J.

- '12 Phototaxis of the Sea Urchin *Arbacia punctulata*. *Jour. Anim. Behavior*, Vol. 2, pp. 126-136.

Jennings, H. S.

- '07 Behavior of the Starfish *Asterias forreri* de Loriol. *Univ. California Publ. Zool.*, Vol. 4, pp. 53-185.

Jensen, P.

- '93 Ueber den Geotropismus niederer Organismen. *Arch. ges. Physiol.*, Bd. 53, pp. 428-480.

Kanda, S.

- '14 On the Geotropism of *Paramecium* and *Spirostomum*. *BIOL. BULL.*, Vol. 26, pp. 1-24.

Lyon, E. P.

- '05 On the Theory of Geotropism in *Paramecium*. *Amer. Jour. Physiol.*, Vol. 14, pp. 421-432.

Moore, A. R.

- '10 On the Righting Movements of the Starfish. *BIOL. BULL.*, Vol. 19, pp. 235-239.

Olmsted, J. M. D.

- '17 Geotropism in *Planaria maculata*. *Jour. Anim. Behavior*, Vol. 7, pp. 81-86.

Pearl, R.

- '02 The Movements and Reactions of Fresh-Water Planarians. *Quart. Jour. Micr. Sci.*, Vol. 46, pp. 508-714.

Ritter, W. E., and G. R. Crocker.

- '00 Multiplication of Rays and Bilateral Symmetry in the 20-rayed Starfish *Pycnopodia helianthoides* (Stimpson). *Proc. Washington Acad. Sci.*, Vol. 2, pp. 247-274.

Small, J.

- '20 A Theory of Geotropism. *New Phytologist*, Vol. 19, pp. 49-63.

Small, J.

- '21 The Hydrion Differentiation Theory of Geotropism: a Reply to some Criticisms. *New Phytologist*, Vol. 20, pp. 73-81.

Verworn, M.

- '89 Psycho-physiologische Protisten-studien. Jena, VIII + 219 pp.

Zollikofer, C.

- '18 Ueber das geotropische Verhalten entstärkter Keimpflanzen und den Abbau der Stärke in Gramineen-Koleoptilen. *Ber. deut. bot. Gesell.*, Bd. 36, p. 30.